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MSS. intended for publication and books, etc., intended for review should be sent to Professor J. McKeen Cattell, Garrison-on-Hudson, N. Y.

GEOGRAPHICAL DISTRIBUTION OF THE MARINE ALGÆ[1]

IN connection with some work I am attempting along the line of geographical distribution, it has become desirable to make some sort of a survey of the entire literature of the marine algæ, to classify it and to note the influence of various writers in developing the different lines of geographical study. The progress of the knowledge of the marine algæ has been slow in comparison with that of most other groups and the progress of our knowledge of the geographical distribution has been slower still. Much of this is due to the comparatively limited access to living material, the difficulties of collection, and the lack of any extensive economic value.

In attempting to arrange the literature, as indicating the progress of thought and development, it has seemed best to separate the lines of work formally, and somewhat arbitrarily, into several more or less distinct, yet necessarily overlapping and intertwined groups of subjects. The subjects finally selected as bearing either directly or secondarily on geographical distribution are five, viz., taxonomy, morphology and development, floristics, physiology and geographical distribution. It is, of necessity, an impossible matter to segregate all the literature and arrange it definitely under one or another of these groups. Certain writers have written along two or more of these lines and in the later literature, particularly, several lines of thought and

[1] Address of the vice-president and chairman of Section G, Botany, American Association for the Advancement of Science, New York, December 27, 1916.

research are often found in combination. Nevertheless, both writers and works, as a rule, follow a main trend and may be arranged under one or another of the principal subjects, although important contributions under a different subject may also be included. Each of the subjects, in turn, may be divided into periods according to the principal influence at work and the progress along a special line of development. One period naturally passes over into another, the way being prepared by those writers whose work may be termed anticipatory and the inception of a new period being marked by some writer, or group of writers, whose advance is more pronounced and whose innovations have had the greatest influence. In taxonomic lines, the beginnings are to be found in the earliest writers, both botanical and non-botanical, and the progress in the study of the marine algæ was necessarily slow until the study of more and more of the more complex plants had pointed the way and, to some extent at least, the methods.

Naturally the earlier work on the marine algæ, as on higher plants, was taxonomic, particularly descriptive. In the earlier period mere mention was made in general, but Morison, Ray, Hudson, Dillenius and Linnæus, for example, laid the foundations upon which Goodenough and Woodward, Gmelin, Turner, Esper, Poiret, De Candolle and others built more solidly. Gmelin (in 1768) published the first book on marine algæ, entitling it "Historia Fucorum." In the latter portion of this first period Roth and Stackhouse prepared for the coming of a more logical treatment, especially as to genera. The older method divided the species of algæ between such polymorphic and indefinite genera as *Fucus, Ulva, Conferva, Byssus* and *Tremella*. Roth and Stackhouse added a few new ones, but these are also mostly of extensive application and of indefinite character.

The second period of taxonomic progress dates from 1813, when J. V. Lamouroux published his "Essai sur les genres de la famille de Thassiophytes non articulées." Lamouroux practically instituted genera in very much the modern sense and laid the foundation for future work. Henceforth both the general morphology and the character of the fructification were taken into account in taxonomic work. Besides Lamouroux Bory de Saint Vincent, C. A. Agardh and Lyngbye were responsible for advance in the earlier part of this second taxonomic period. They were succeeded by Greville, Montagne, Decaisne, J. G. Agardh, J. D. Hooker, W. H. Harvey, Kützing, J. E. Areschoug, Ardissone, Zanardini, Ruprecht and others.

The latter part of the second taxonomic period is merged with and came under the influence of a more careful morphologic and histologic study and a closer attention to the structure and development of the organs of fructification. Kützing did much to promote this in his "Phycologia Generalis" (1843) and his "Tabulæ Phycologicæ" (1845–1869). Naegeli, Cramer, Zanardini and others assisted in the same direction. These works mark the passing over into the third distinct taxonomic period which may be said to have begun with Thuret and Bornet and which has continued down to our own times. Its earlier inquiry into the nature of the reproductive bodies dates from Thuret's classic researches on the zoospores and antheridia of the algæ (1845–1855). This was continued into the discoveries as to the modes of development of the cystocarp in the red algæ and all came as a culmination of the similar work by Pringsheim, Naegeli and others. The magnificent "Notes Algologiques" (1876, 1880) and "Etudes Phycologiques" (1878) will long remain as examples of the finest contributions along these various lines of histolog-

ical and developmental researches. The progress along this line has led to other studies of histological and developmental details. These in turn have led up to the present condition, when it seems desirable to make a new and more detailed study of all species, but especially of those credited with a wide geographical distribution or with great variability.

The third and latest period of taxonomic development has resulted in a newer view of specific limitation, in other words, has resulted in specific segregation being carried to a much greater degree than hitherto, yet seemingly not beyond reasonable limits. The results may be seen from Kjellman's treatment of *Galaxaura* (1900), Falkenberg's treatment of the *Rhodomelaceæ* (1901), A. and E. Gepp's treatment of the *Codiaceæ* (1911), Sauvageau's treatment of the *Sphacelariaceæ* (1900–1914), Howe's treatment of *Halimeda* and other genera (1905–1914) as well as of other groups, Foslie's treatment of the crustaceous corallines, Boergesen's treatment of the algæ of the Danish West Indies (1913–1916), my own treatment of *Scinaia* (1914), and others. In my own study of various genera of the red algæ, both from the point of view of morphological differences and of geographical distribution, it is necessary to more carefully distinguish and separate the true species in the case of many aggregates and to scrutinize very carefully those species credited with extended or widely discontinuous distribution. The results throw a much clearer light on certain seemingly troublesome points of geographical distribution, both climatic and topographical.

The anatomical and histological aspects of the morphology of the marine algæ were earlier treated of in connection with the taxonomy. In the first period of taxonomy, the study of the structure both of the vegetative and reproductive portions was slight, although some progress was made through Reaumur (1711), Stackhouse, Turner and others. In the second taxonomic period, Lamouroux gave a great impetus to the study of structure and the distinctions between the different methods of fructification and towards the last of this second period the knowledge of structure was placed on a fairly firm basis.

It was during the third taxonomic period that the study of morphology may really be said to have originated as a separate subject and much of the credit for properly emphasizing it came from Thuret, both by his own publications and by those in connection with Bornet. Since then many special papers dealing with the adult or developmental morphology have been published. Cytological work, too, has been carried on to a considerable extent. The cell membranes have been studied by Correns and others; the chromatophores by Schmitz and his successors; various cell contents, including the plasma massing in the cells of iridescent marine algæ by Berthold and others. The study of the nucleus and its division has engaged the attention of many investigators from Schmitz (1879) through Fairchild, Swingle, Farmer, Strasburger, Osterhout, Williams, Wille, B. M. Davis and Oltmanns. Yamanouchi and Svedelius, in particular, have investigated the chromosome number in connection with the alternation of generations of red algæ. The morphology, both gross and minute, of holdfasts, vegetative and reproductive organs, have been, and still are being, given most careful attention, in connection with taxonomic, physiological and ecological investigations.

While most attention has been turned towards the morphology and development of the marine algæ, their special physiology has received some attention. By far the greater portion, however, remains to be done. It is impossible to more than call

attention to some main lines of work in this communication. The physiological effects of the pigments by Gaidukov, Rosanoff, Reinke, Schütt and Kylin; metabolic activities of various sorts such as those dealt with by Loew and Bokorny, by Hansen, Wille, Arber, Artari and a host of other investigators; the physiology of reproductive processes by Klebs; the method of production of lime incrustations by Lütgeb; the influence of external surroundings by Oltmanns. The physiologico-anatomical researches of Wille and his pupils may be mentioned here. The influence of light, temperature, specific gravity of the sea water, chemical stimuli, etc., have been touched upon by various authors, but these important physiological bases for explaining the facts of geographical distribution and particularly of ecological distribution are still most obscure.

To deal with the geographical distribution of plants it must be recognized that there are several methods of approach, and in dealing with the geographical distribution of the marine algæ, the methods of approach are, in general, the same as those used in dealing with other plants. The first efforts are floristic and usually largely taxonomic. Species are defined more and more accurately and floras are made out for larger or smaller coast lines. Then comes a comparison of floras with one another as to percentages of common or differing species. Cosmopolitan or widespread species are discussed, as are also endemic species, or at least species of more restricted areas and finally the comparison of floras leads to a discussion of the relation of floras as to origin, spread, etc.

Less has been done in the floristics of marine algæ than in that of terrestrial plants. There are comparatively few floras, although many lists have been published. One of the earliest marine floras or lists was that of Goodenough and Woodward for the British Fuci (1797) in which only 72 species were described. This was followed by that of Turner (1802), who enumerated and described 78 species. These included only the species of *Fucus* as then understood. Greville in his Algæ Brittanicæ (1830) greatly increased the number and Harvey in the two editions of his Manual (1841 and 1849) as well as in the Phycologia Brittanica (1846–1851) brought the number up to 388, while Holmes and Batters in their lists of British Algæ (1890, 1891) enumerate 557 species. C. A. Agardh's Synopsis Algarum Scandinaviæ (1817) is another early algal flora as is also Lyngbye's "Tentamen Hydrophytologicæ Danicæ" (1819). More modern is the "Algues Marines du Cherbourg" (1864) of A. Le Jolis and one which has had great influence as a model. One of the earliest accounts to contain a direct comparison between a particular marine flora and other marine floras is Farlow's "Marine Algæ of New England" (1881), in which the comparison is made in the percentage of species between the various subdivisions of the New England coast and also between them and the flora of various parts of Europe, of the Arctic Regions and of the Pacific Coast of North America. Martens (1866) had previously made such a comparison in detailed list between various divisions of the tropical marine flora. Other writers have attempted to classify floras as to their content of species common to or characteristic of other regions as well as those confined to their own region. The most formally floristic papers as to geographical distribution of marine algæ are those of George Murray on "A Comparison of the Marine Floras of the Warm Atlantic, Indian Ocean and the Cape of Good Hope" (1894) and of George Murray and E. S. Barton on "A Comparison of the Arctic and Antarctic Marine Floras" (1895). These papers deal with the percentage of endemic species and

of those common to two or more subdivisions and lay particular stress on the relative number of species to the genus in the various geographical divisions or subdivisions.

The results of this purely floristic work on the marine algæ has been, just as has happened more extensively in phænogamic floristics, the separation of floras more or less distinctly marked off from one another and in some cases the discovery of definite demarcation points. As illustrations of this may be mentioned the following: the Arctic and Mediterranean marine floras were readily understood, but the intermediate floras were not distinguished, nor were there any sharp points or districts of demarcation discovered. The marine flora of the Cape of Good Hope region has always been recognized as very distinct, but the exact limits have never been determined. On the eastern coast of North America, on the contrary, and especially on the coast of New England, not only was the northern flora recognized as different from that of Long Island Sound and southward, but also the Cape Cod Peninsula was indicated as the region of demarcation between the two. This was first mentioned by W. H. Harvey in the first part of the "Nereis Boreali-Americana" (1851). Harvey divides the east coast of North America into 4 divisions, viz., "First, the coast north of Cape Cod, extending probably to Greenland; second, Long Island Sound, including under this head New York Harbor and the sands of New Jersey; third, Cape Hatteras to Cape Florida;" and "fourth, Florida Keys and shores of the Mexican Gulf." This dividing up of the marine flora of the eastern coast of North America is the first division of any definiteness for that of any extended coast and corresponds fairly closely to the zones of the marine flora into which my own investigations indicate it should be divided. Harvey's statements in the "Nereis Boreali-Americana" result from his ideas formulated in the second edition of his "Manual of the British Marine Algæ" and are a direct application of the earlier ideas of Lamouroux (1825, 1826). Along with the separation of floras is a comparison, as to similar latitudes and isothermal lines, between the east coast of North America and the coasts of Europe, but these isotherms are lines of mean annual temperature and likewise are those of the air, but not of the water, indeed for application to land floras, and not affecting, as a whole, at least, the marine flora. This work of Harvey was the first detailed attempt to associate floristic methods with the factors which control climatic distribution.

Later developments of the floristic idea are to be found in Kjellman's work, especially in the "Algæ of the Arctic Sea" (1883) and in the works of Simmons (1897) and of Börgesen and Jönsson (1905) on the marine flora of the Faeroes and the North Atlantic. The Baltic Sea was studied as to its marine flora by Reinke (1889), Svedelius (1901), and Kylin (1906, 1907), that of New England by Farlow (1881) and Collins (1900), that of Iceland by Jönsson (1912), tropical floras of the Indian and Pacific Oceans by Schmitz (1896) and Schroeder (1902), and the antarctic floras by Gain (1912). All these works have been along the same general lines.

To sum up the results of the floristic work, general climatic regions have been set off and distinguished from one another, methods of and agents in dispersal have been discussed, demarcation points between floras have been determined, centers of distribution have been emphasized, and barriers to dispersal have been surmised. All these lead toward the discussion of climatic distribution and to some extent toward that of topographical distribution or ecology. Yet these are all more floristic in style and

point of view than from the standpoint of geographical distribution in relation to definite factors controlling it.

The idea of geography as applied to plant life, while present in indefinite form in the treatises of the Greek period, came as a revolutionary idea to the German Fathers and their immediate successors. It was Alexander von Humboldt, however, who, early in the nineteenth century, gave the first real impulse to the idea of the study of the geography of plants (1805) and the climatic conditions, climatic zones and altitudinal zones which are to be associated with, and to be taken account of in connection with it. It was J. V. Lamouroux, however, who first formulated the outline of topics connected with the distribution of "Hydrophytes" (marine algæ) in 1825 and 1826. Lamouroux had for his models the works of von Humboldt, A. P. De Candolle and Robert Brown on "Aerophytes." It is of interest to notice the topics brought forward by Lamouroux. In the first place, the basis for his study, as he states, consists of some 1,200 species of his own collections and those of the various botanists of Paris, and including specimens collected in many voyages to distant parts of the world. He touches upon species which are, in a sense, cosmopolitan and speaks of the Ulvaceæ or sea lettuce family, as being distributed from the poles to the tropics. This is particularly in connection with the temperature factor and he remarks that the number of species is greater in the temperate zones than in the very cold or very warm zones. In treating of the distribution of families, he makes the point that because of the configuration of coast lines, their distribution from a center is linear rather than radiating as in land plants. He mentions seasonal temperature effects in that the period of higher temperature in any locality shows the greater number of species. He also suggests that possibly the depth relation to distribution is the same as the altitudinal relation to land floras and that there may possibly be expected an arctic or frigid marine flora in the depths of tropical waters, as a frigid land flora is found on high peaks in warm zones. Lamouroux takes up the influence of light, of the aeration of the water and of the plant exposed more or less often and more or less completely by the ebb and flow of the tides. The substratum receives some attention from Lamouroux and also a considerable attention is given to the distribution of the particular divisions and families. Altogether Lamouroux has treated of a considerable number of facts and factors underlying even the more modern consideration of the subject. Greville (1830) and W. H. Harvey (1849, 1851), as has already been stated, have followed Lamouroux and have treated of the geographical relationships of the various floras, but chiefly from the point of view of floristics. Lamouroux and Harvey laid the chief emphasis on general climatic factors, of which temperature is by far of widest effect and importance, and this view was followed by the later writers, who associated factors with their floristic treatment. A new impetus was given the study of climatic distribution by Kjellmann's various papers, particularly by "The Algæ of the Arctic Sea" and the later subdivisions of the Polar Sea. The discussion of the marine floras of the North Atlantic at the hands of Reinke, Simmons, Boergesen and Jönsson simply emphasizes the importance of this climatic factor or sets of factors.

Before leaving this more general treatment, it may be well to speak of Piccone's work (1883) as the only general treatise, other than that of Lamouroux, on the geographical distribution of the marine algæ. Piccone treats of the general features of an algal flora and the general conditions, such as the substratum, both as to physical and

chemical aspects as well as the modes of attachment to and the various methods of aggregation of the algæ on it. He considers also the aspects of chemical composition and variation in salinity of the sea water, as well as its purity, its gas content, its density and its color. There follows a discussion of the influence of the temperature of the water, of the influence of light, of color of the water, of methods of dispersal by currents and by fishes, of the nature of spores, etc. Finally the general organization of the plants themselves is dealt with.

Under the head of climatic distribution and with the controlling factor of temperature in mind, may be mentioned my own papers on this subject in 1893, 1903 and 1914, respectively, where there is an attempt made to outline certain climatic zones depending primarily upon the mean temperature of the surface waters. In these papers I have treated in a general and preliminary way of temperature zones, 5° C. apart, as to surface waters and mean maximum temperature. I have also briefly touched upon the invasions of these zones at seasons of other temperatures, particularly at the mean minima, by species from other zones. These invasions account for much of the seeming disturbances of uniformity and exclusiveness of flora. I am now prepared to account for other invasions due to the raising of temperature of the algæ in tidal belts and in shallow areas, such as salt lagoons and estuaries through the temperature of the air. Through these factors practically all invasions or overlappings from one zone into another, may, as it now seems to me, be explained.

Turning from the papers which are generally floristic or which deal only with the general climatic factors, there are certain papers dealing with the topographical or ecological distribution. While Lamouroux hinted at certain features such as the influence of aeration in the tidal belts and the influence of the substratum, the first papers to deal with topographical features of distribution for marine algæ were those of J. G. Agardh (1836) and Oersted (1844). Both divided the shore belts of the Danish and southwest Swedish coasts into three regions, the uppermost characterized by a predominance of the green algæ, the middle by the predominance of brown algæ, and the lowermost by that of the red algæ. Oersted, however, was the first to attribute this division into regions to a definite influence, viz., to the light as to depth penetration and as to color. Kjellman, later and in several papers, also divides the shores generally into three "regions," the littoral, the sublittoral and the elittoral. He also developed the idea of algal formations, or, as they are more properly called, of "associations." In both these segregations, Kjellman is followed by most later writers.

Rosenvinge for Greenland, Boergesen for the Faeroes, Kylin for the western coast of Sweden and Jönsson for Iceland have applied and extended the ideas of Kjellman as to topographical units and the factors controlling them, as well as for factors of climatic importance. Jönsson (1912) has given a particularly complete and satisfactory outline and discussion.

Schimper, Warming and Clements have given classifications of the marine, as well as the fresh-water algæ, distinguishing the plankton or swimming forms from the benthos, or attached forms, and, in distinguishing the benthos formations according to the substratum, viz., as to sand or rock and in making even farther distinctions.

Two papers of recent date contain data and observations of great importance in topographical distribution of the marine algæ. One of these is the contribution of B. M. Davis (1913) to the "Biological Survey of the Waters of Woods Hole and Vicinity," while the other is the paper of K.

Yendo (1914) "On the Cultivation of Seaweeds with Special Accounts of their Ecology." In each of these papers attention is called to ecological factors modifying or illustrating the workings of general factors of distribution as well as those concerned in special topographical distribution.

To sum up the general results and to attempt to determine the general subdivisions of the coast lines to satisfy all requirements of geographical distribution, the following seems to be a reasonable, although tentative, arrangement, both as to climatic and as to topographical divisions.

CLIMATIC

I. *Zones,* regulated by temperature of the warmer months, especially to be determined by the mean summer temperatures or in practise by the isotheral lines at intervals of 5° C.;

II. *Regions,* purely geographic segregations under zones;

III. *Provinces,* subdivisions of regions according to mean winter temperatures, in practise by isocrymes, 5° apart or less;

IV. *Districts,* subdivisions under provinces according to geographical remoteness and varying physical conditions of a general nature;

TOPOGRAPHICAL

V. *Formations,* aggregations of algæ of same general form, depending particularly upon substratum;

VI. *Associations,* aggregations of algæ depending for general likeness of plant form, etc., on depth (belts), salinity, light, aeration, etc., generally characterized by the predominance of a single, or at most, of a few species.

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THE CARNEGIE INSTITUTION OF WASHINGTON AND SCIENTIFIC RESEARCH[1]

Numerous references have been made in preceding reports to the growing realization of the world at large that the methods of science are the most effective methods thus far developed for the advancement of learning and for the mitigation of the consequences of the inexorable "laws of nature" which condition existence on our planet. Reference has been made likewise to the contemporary rise and progress of other research establishments and to the introduction of investigation as an economic adjunct to industrial enterprises. These manifestations of popular approval and confidence continue to be among the most noteworthy signs of the times. Indeed, it is plain that we are now witnessing a remarkably rapid evolution of public understanding of the meaning and the value of research. This has been greatly intensified and accelerated by the European war, whose sinister aspects appear to be relieved in some degree by the prospects of an awakened realization of the availability of better methods than those of warfare for settling international disputes, of better methods than those now commonly applied in the government of states, and of better methods in education, in sanitation, in industry, and in biological economy generally. The European war has emphasized to a degree not hitherto attained in the world's history the perils of ignorance, of government by assumed divine right, and of that sort of diplomacy which shades off by insensible degrees into duplicity; and it has emphasized equally clearly the necessity for rational investigation of and progressive reforms in all national affairs.

How the details of this evolution, in which the institution must participate, will

[1] From the report of the president for 1916.